NOTES ON SKELETAL VARIATION, TOOTH REPLACEMENT, AND CRANIAL SUTURE CLOSURE OF THE PORCUPINE (*ERETHIZON DORSATUM*)

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ABSTRACT

Variation occurs in many of the cranial elements and in the pattern of the cranial foramina of the porcupine *Erethizon dorsatum*. Tooth eruption and replacement are completed by the end of the second year of life with all molars erupting by the age of 6–8 months and the deciduous premolars replaced between 12–18 months later. Sutures of the skull close in a predictable pattern and closure is correlated with age. Variation in the vertebral number is considerable, with the thoracolumbar region varying from 19–23. The presence of one major sesamoid in the carpals and two in the tarsals has led to some confusion in the terminology used by previous writers.

INTRODUCTION

Information on the osteology of the porcupine (*Erethizon dorsatum*) is not plentiful in the literature. Only Swena and Ashley (1956) have discussed the skeleton at some length. This paper offers new information, particularly with respect to variation, and discusses certain points which are in disagreement with earlier writers. The sequence of suture closure and the timing of tooth eruption and replacement are briefly outlined.

METHODS AND MATERIALS

For this study 186 cleaned skulls and 26 complete skeletons were examined. Data presented here are largely qualitative and are intended to show areas in which variation was easily noticed. In studying vertebral variation, only complete skeletons which were either articulated or semi-articulated in such a manner that all vertebrae could be accounted for were used.

Deciduous and permanent teeth were distinguished by observation of the root position in the upper premolars and by occlusal patterns in the lower premolars. Several X-ray photographs were taken on doubtful specimens, but this was usually unnecessary. Permanent premolars were generally larger than deciduous premolars.

Suture closure was determined by the amount of ossification along a suture. A suture was considered closed if one-half or more of its length was ossified.

Specimens examined were from collections at: University of Nebraska (ZM); University of Kansas Museum of Natural History (KU); United States National Museum (USNM); the American Museum of Natural History (AMNH); Southern Illinois University (SIU); University of Arizona (UA); Chicago Field Museum of Natural History (FMNH); National Museum of Canada (NMC); Peabody Museum Yale University (YPM); University of Utah (UU); as well as two personal specimens (JFS). A complete list of the specimens examined is available in the manuscript on file at the Southern Illinois University Library.

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Osteological Variations and Observations

THE SKULL

Frontal.—The frontals often bear raised areas over the orbits which appear to vary with age. These bulges are more pronounced in older males than in females although they can be equally developed in both sexes. Those animals in the Western United States, particularly *Erethizon dorsatum epixanthum*, tend to have larger bulges than any of the other subspecies.

Parietal.—The coronal suture (anterior suture) separating the parietals and frontals varies individually in the specimens examined. In some skulls the coronal and sagittal sutures intersect at nearly 90°, while in others they may form an inverted "V" where they meet. A complete gradation in variation is seen between these two extremes.

Interparietal.—The interparietals are usually triangular, with the base along the occipital suture on the lambdoidal ridge. Variation in shape of the interparietals is caused by the formation of wormian bones, which may number as many as eight, along the sagittal suture. These wormian bones may also continue forward along the sagittal suture into the parietal and frontal area.

Occipital.—The external occipital protuberance projects posteriorly as an apparent extension of the sagittal crest through the lambdoidal ridge. This is also a function of age, with the protuberance being largest on the oldest individuals.

Squamosal.—The posterior margin of the squamosal may articulate with the occipital along the lambdoidal ridge or, less commonly, with a lateral extension of the parietal.

Swena and Ashley (1956, Fig. 1) indicate that a separate temporal bone and a distinct squamosal exist in the porcupine. Romer (1963) points out that when a temporal bone exists, it is a compound structure composed of the fused squamosal, periotic, and auditory bulla (tympanic). In the specimens which I have examined, fusion of these elements has not occurred except in several extremely old specimens.

Swena and Ashley illustrate two bones in the squamosal area and identify the anterior bone supporting the zygoma as the squamosal, and the posterior bone over the bulla as the temporal. This is probably the result

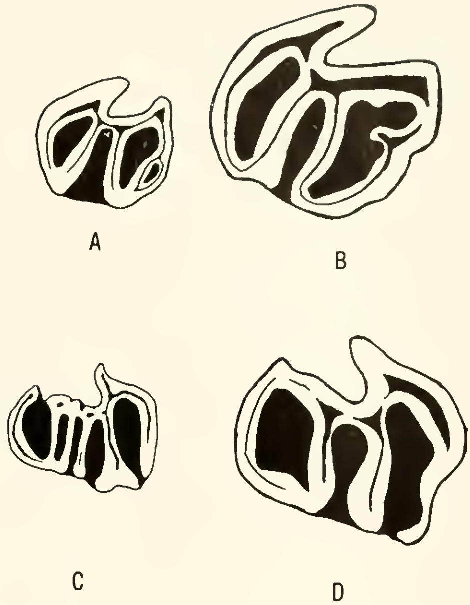

Figure 1. Deciduous and permanent premolars of *Erethizon dorsatum*. A. dp^4. B. p^4. C. dp$_4$. D. p$_4$. All figures 4, 5×.

of a second center of ossification in the squamosal area. I observed one specimen (AM63759) which showed two "squamosals" that was undoubtedly the result of two centers of ossification in the squamosal area.

Lacrimal.—In most mammals the lacrimal bone occupies the anterodorsal margin of the orbit. The porcupine apparently lacks this bone since few of the specimens possessed a suture which could be identified as a lacrimal suture. It is possible that this bone is formed and fused to the maxillary during embryonic development; however, Struthers (1927) does not indicate the presence of this bone in the early embryology.

Jugal.—The jugal bone, zygomatic process of the maxillary, and zygomatic process of the squamosal form the zygomatic arch in the porcupine. The arches are usually slightly asymmetric, with the left arch extending further posteriorly than the right. This usually results in a thinning and more pronounced recurving of the left zygomatic process of the squamosal.

Cranial foramina.—The cranial foramina of the porcupine and other rodents have been summarized by Hill (1935). Some addi-

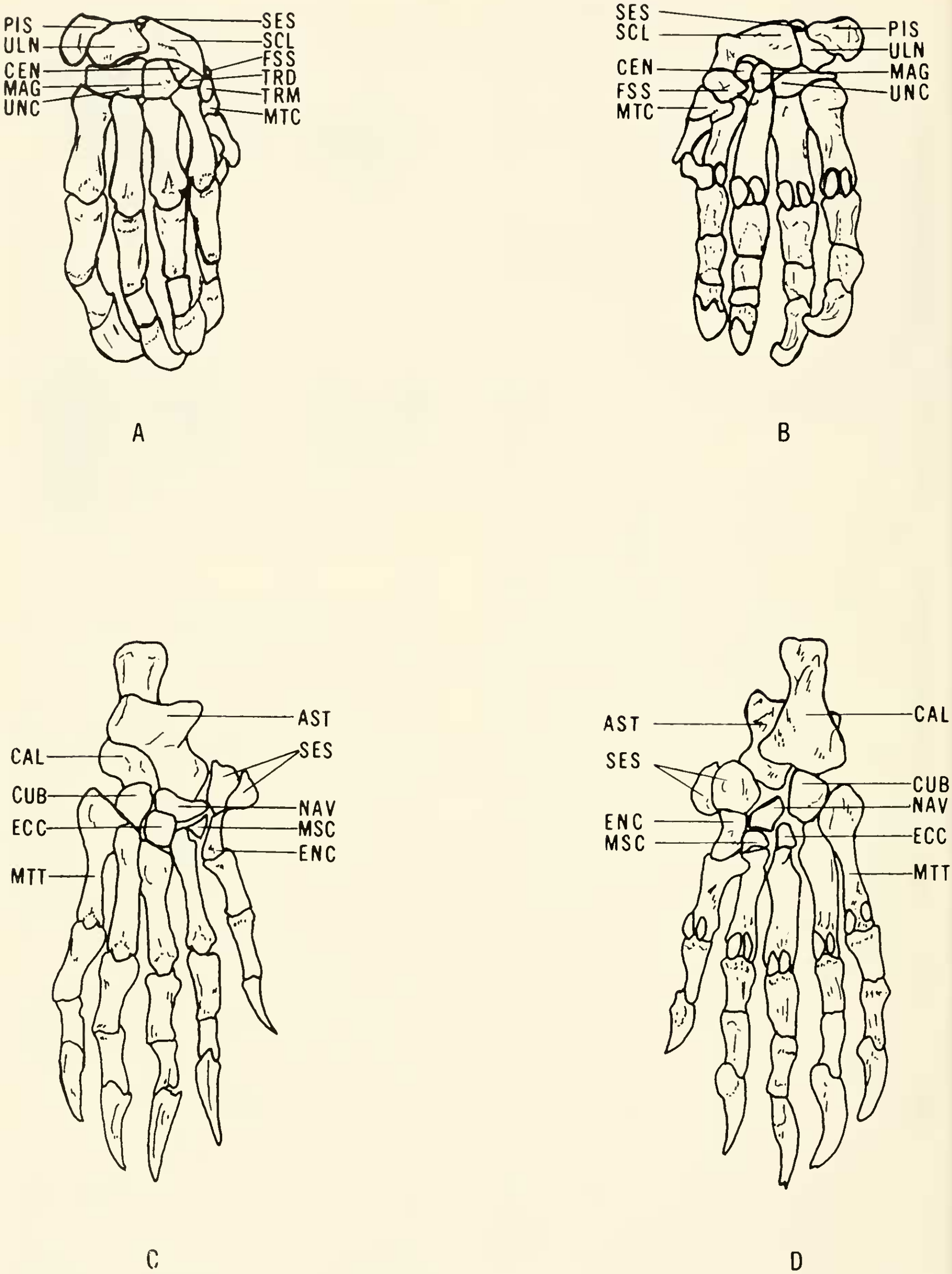

Figure 2. Carpals and tarsals of the porcupine *Erethizon dorsatum*. A. Dorsal view of the carpals. B. Ventral view of the carpals. C. Dorsal view of the tarsals. D. Ventral view of the tarsals. All figures 1×. Abbreviations. AST.—astragalus, CAL.—calcaneum, CEN.—centrale, CUB.—cuboid, ECC.—ectocuneiform, ENC.—entocuneiform, FSS.—falciform sesamoid, MAG.—magnum, MSC.—mesocuneiform, MTC.—metacarpal, MTT.—metatarsal, NAV.—navicular, PIS.—pisiform, SCL.—scapholunar, SES.—sesamoid, TRD.—trapezoid, TRM.—trapezium, ULN.—ulnare, and UNC.—unciform.

tional information can be added here concerning variation in these foramina.

The masticatory and buccinator foramina are extremely variable. According to Hill, the two are separate; however, I found that confluence of these foramina is common.

The squamosal foramen is absent in the porcupine according to Hill; however, I found it in the majority of my specimens. In some individuals the foramen was absent, or present on one side of the skull only. The interpremaxillary foramen (Hill, 1935) is not located in the typical position in the porcupine. Hill describes this foramen in other rodents as being located immediately posterior to the incisor teeth in the premaxillary. In the porcupine it is located immediately anterior to the palatine foramina and may be paired in some individuals.

The nasolacrimal canal of the porcupine is well developed although somewhat unusual in its pathway according to Hill. In some of the specimens I examined, the canal was either completely lacking or represented by a small depressed area in the maxillary.

Tooth eruption and replacement.—According to Taylor (1935) most porcupines are born in April and May with occasional births occurring later in the summer. The tooth complement at birth includes an incisor, deciduous fourth premolar, and first molar in each tooth row.

The second molar begins to erupt in August of the first year, but may not appear until October. Eruption is complete by October in most cases. The final molar appears in mid-winter of the first year.

Following the eruption of the molars, a period of 12–18 months passes before the permanent premolar replaces the deciduous premolar. Premolars in the process of replacement were observed in ten specimens; six were in mid-winter of the second year and four were starting their third summer of life (Sutton, 1969).

Differentiation between permanent and deciduous premolars (Fig. 2) in the maxillary was accomplished by examining the visible root areas in the prepared skulls. The DP^4 and P^4 are identical in occlusal pattern; however, the DP^4 differs in the degree of spreading of the roots to allow for development of the P^4 in the maxillary. DP_4 and P_4 are different in occlusal pattern with DP_4 being narrower and composed of six enamel bands, while P_4 is composed of four (occasionally five, KU62282).

TABLE 1. Suture closure. Percentage and total number of animals with specific sutures closed. Based on 184 animals.

Suture	Percent	Number closed
Occipital-parietal-interparietal	88.0	162
Interparietal-interparietal	84.8	156
Parietal-interparietal	77.7	143
Parietal-parietal	60.9	112
Parietal-frontal	39.1	72
Frontal-frontal	37.0	68
Frontal-squamosal	31.5	58
Parietal-squamosal	31.0	57
Nasal-nasal	12.5	23
Premaxillary-maxillary	08.7	16
Frontal-nasal	05.4	10
Jugal-zygomatic of squamosal	04.9	9
Frontal-maxillary	04.3	8
Zygomatic of maxillary-jugal	04.3	8
Frontal-premaxillary	02.0	4
Nasal-premaxillary	00.5	1

Suture closure.—Suture closure was examined and recorded in 184 skulls. Sixteen skulls with no sutures closed are presumed to be from animals less than four months old. Table 1 lists the sutures (identified by the bones lying on either side), the percentage, and the total number of specimens with that suture closed. The apparent groups into which they fall presumably correspond to yearly growth (see Sutton, 1969). These data were also submitted to multilinear regression (Kelly *et al.*, 1969) to establish correlation values. The relationships which resulted corresponded closely to those represented by the percentage system (Table 1) and need not be repeated here.

Four sutures close during the first year of life. These include: occipital-parietal-interparietal; interparietal-interparietal; parietal-interparietal; and parietal-parietal. These sutures are associated with the closure of the braincase and probably reflect completion of brain development.

Second year individuals are characterized by continued completion of skull growth in an anterior direction. Skull width is complete (except zygomatics) and the skulls are approaching adult size. The sutures involved include: parietal-frontal; frontal-frontal; frontal-squamosal; and parietal-squamosal. The nasal-nasal suture follows these in percent of closure, but is seldom completely closed. Ossification begins at the rear or base of the nasals and progresses anteriorly. This suture and the remaining sutures (with the exception of the zygomatics) are all related to the nasal area and close slowly throughout the remainder of the life of the animal. This probably reflects a slow widening and lengthening of the skull in the nasal area accounting for most of the variation in skull length of adult animals.

From this point on closure of the remaining sutures is slow, with the zygomatic of the squamosal-jugal and zygomatic of the maxillary-jugal closing very late in the life of the animal.

THE POST-CRANIAL SKELETON

Vertebral column.—Variation in the number of vertebrae has been reported for many animals, especially in the caudal region where loss of vertebrae is common. Occasionally variation is reported within the thoracolumbar region, but this usually results in a nomenclatorial problem since the loss of a rib pair is generally the source of the variation. A few animals do vary in the total number of thoracolumbar vertebrae, but this variation usually involves a difference of only one vertebra, seldom more.

Swena and Ashley (1956) indicate the vertebral formula of the porcupine to be: c_7 th_{15-16} l_7 s_4 ca_{14}; whereas Gupta (1965) indicates that the formula is c_7 th_{15-16} l_5 s_{3-4} ca_{18}. Gupta also maintains that when 16 thoracics are present, only three sacrals will be found. In this study four sacrals were consistently observed with the fourth sacral connected to the ischial tuberosity of the innominate by a ligament.

Thoracic vertebrae and the number of associated pairs of ribs varies from 14–17. Occasional skeletons exhibit a small rib (25 mm or less) on the last thoracic vertebra. This small rib may be normally articulated on both sides, or on one side only with fusion to the vertebra on the other. The vertebra in question was assigned to the thoracics when this situation was found.

Lumbar vertebrae vary in number from five to six, and variation is not correlated with an increase or decrease in thoracic number as Gupta indicated concerning the thoracic-sacral situation. I found no specimens with seven lumbars as indicated by Swena and Ashley, nor any with 18 caudals as indicated by Gupta.

The total number of thoracolumbar vertebrae varies from 19–23. Table 2 presents the vertebral counts and identification of the specimens involved in the study. Several specimens did not have the caudal region intact, and these figures are omitted.

Carpals and metacarpals. Figures 2a and 2b. Metacarpal I is extremely reduced. The sesamoids, which are obvious on the metacarpal-phalanx arcticulations of other digits, are extremely reduced, but still present.

Swena and Ashley (1956, Figs. 26 and 27) report the existence of a greater multangular and trapezium in the carpus of the porcupine. These two names are synonymous. That which they identify as the greater multangular is in reality a sesamoid. Howell (1926) describes a similar sesamoid in the wood rat and applies the term falciform sesamoid to the bone.

Tarsals and metatarsals. Figures 2c and 2d. The interpretation of the tarsal elements of the porcupine appears to be particularly troubling due to the presence of two sesamoids on the medial margin of the foot. Hill (1937) recognized an extra sesamoid in the foot of the pocket gopher and termed it the *os tarsale mediale.* I have not attempted to name either of the two elements, but have chosen to refer to them as sesamoids until further anatomical work can be done.

I do not agree with Swena and Ashley in naming these elements the tibiale and the first cuneiform for several reasons. The internal sesamoid articulates with the head of the astragalus internally, and externally with the other sesamoid. It articulates with the entocuneiform distally. This internal sesamoid is that referred to as the tibiale by Swena and Ashley. The tibiale is not found in mammals, but is one of the primitive reptilian bones forming the astragalus (for example, Peabody, 1951, in *Captorhinus*). In reality this sesamoid probably represents part if not all of Hill's *os tarsale mediale.*

The external sesamoid is called the first cuneiform (entocuneiform) by Swena and Ashley. If this bone is to be considered an entocuneiform, the remaining tarsal elements are indeed extremely modified. Swena and Ashley indicate that metatarsal I is in the position of the entocuneiform and is ex-

TABLE 2. Vertebral variation in the porcupine *Erethizon dorsatum*. Abbreviations: Ca., Caudal; L., Lumbar; and Th., Thoracic.

Number	Th.	Th.–L.	Ca.	L.	Sex	Location	Subspecies
KU 9406	17	23	17	6	M	Kan.	*E. d. bruneri*
KU 12098	16	22	15	6	F	Captive	*E. d. dorsatum*
KU 8266	16	21	16	5	?	N. M.	*E. d. couesi*
KU 15859	16	21	16	5	F	Wyo.	*E. d. epixanthum*
AMNH 70015	16	21	15	5	M	?	*E. d. ?*
SIU 0-597	16	21	14	5	F	N. M.	*E. d. couesi*
KU 6645	16	21	—	5	?	N. M.	*E. d. couesi*
ZM 2392	16	21	—	5	?	Neb.	*E. d. bruneri*
KU 7859	15	21	16	6	M	Ariz.	*E. d. couesi*
JFS 4	15	21	—	6	M	Wisc.	*E. d. dorsatum*
SIU 0-471	15	21	15	6	M	Colo.	*E. d. bruneri*
KU 73917	15	21	16	6	F	N. M.	*E. d. couesi*
AMNH 70422	15	21	15	6	M	?	*E. d. ?*
USNM 88619	15	21	15	6	F	N. Y.	*E. d. dorsatum*
ZM 2129	15	21	—	6	M	Wyo.	*E. d. epixanthum*
AMNH 63759	15	21	14	6	F	N. Y.	*E. d. dorsatum*
CFM 53733	15	21	—	6	M	?	*E. d. ?*
KU 15860	15	20	16	5	F	Wyo.	*E. d. epixanthum*
JFS 2	15	20	15	5	M	Wisc.	*E. d. dorsatum*
AMNH 70559	15	20	15	5	M	?	*E. d. ?*
USNM 49420	15	20	13	5	M	Wyo.	*E. d. epixanthum*
KU 8264	15	20	—	5	F	Idaho	*E. d. epixanthum*
AMNH 16872	14	20	16	6	F	?	*E. d. ?*
AMNH 147530	14	20	14	6	F	N. J.	*E. d. dorsatum*
CFM 43299	14	20	—	6	M	Wisc.	*E. d. dorsatum*
AMNH 150093	14	19	15	5	M	N. H.	*E. d. dorsatum*

tremely modified to look more like a tarsal element. That which they call metatarsal I is actually the entocuneiform and therefore should look like a tarsal bone. They state further that there are three phalanges in the first digit, and that the small sesamoids found on the ventral surface of the foot at the metatarsal-phalanx articulation are in a different position on the first digit; between the first and second phalanges with the first phalanx being modified to look like a metatarsal. I feel that there is no need to go to such great lengths to explain the tarsal situation. There are two medial sesamoids which may be the result of splitting of the *os tarsale mediale* of Hill, or they may be of separate origin. Further the entocuneiform is found in its normal position between metatarsal I and the internal sesamoid; metatarsal I is not modified to be a tarsal (functionally); and the first digit has only two phalanges and thus does not differ from the basic mammalian phalangeal count of 2-3-3-3-3.

Literature Cited

GUPTA, BHARAT B. 1965. Skeleton of *Erethizon and Coendou*. Mammalia 30(3):495–497.

HILL, JOHN ERIC. 1935. The cranial foramina in rodents. J. Mammal. 16(1):121–129.

———. 1937. Morphology of the pocket gopher mammalian genus *Thomomys*. Univ. Calif. Publ. Zool. 42(2):81–172.

HOWELL, A. BRAZIER. 1926. Anatomy of the Wood Rat. Williams and Wilkins Co., Baltimore. 225 p.

KELLY, F. J., D. L. BEGGS, K. A. MCNEIL, J. LYONS, and T. EICHELBERGER. 1969. Research Methods in Behavioral Science: Multiple Regression Approach. Southern Illinois University Press. 353 p.

PEABODY, F. E. 1951. The origin of the astragalus of reptiles. Evol. 5:339–344.

ROMER, A. S. 1963. The Vertebrate Body. 3rd Ed. W. B. Saunders Co., Philadelphia. 626 p.

STRUTHERS, P. H. 1927. The prenatal skull of the Canadian porcupine (*Erethizon dorsatus*). J. Morph. Physiol. 44(2):127–216.

SUTTON, JOHN F. 1969. Variation in the skeleton of the porcupine (*Erethizon dorsatum*). Unpublished M.A. Thesis, Southern Illinois University. 146 p.

SWENA, RICHARD, and LAURENCE M. ASHLEY. 1956. Osteology of the common porcupine (*Erethizon dorsatum*). Walla Walla College Dept. Biol. Sci. & Biol. Station. No. 18:1–26.

TAYLOR, WALTER P. 1935. Ecology and life history of the porcupine (*Erethizon epixanthum*) as related to the forests of Arizona and the Southwestern United States. University of Arizona Bull. 6(5):1–177.

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